

Chapter 14

Optimal Tactics of Reproduction and Life-History

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14.1 Introduction

In the game of life an animal stakes its offspring against a more or less capricious environment. The game is won if its offspring live to play another round. What is an appropriate tactical strategy for winning this game? How many offspring are needed? At what age should they be born? Should they be born in one large batch or spread out over a long lifespan? Should the offspring in a particular batch be few and tough or many and flimsy? Should parents lavish care on their offspring? Should parents lavish care on themselves to survive and breed again? Should the young grow up as a family, or should they be broadcast over the landscape at an early age to seek their fortunes independently?

Since even humans seldom think seriously about these questions, it would be silly to pretend that animals literally are scheming tacticians. However, we can still examine the tactical answers to these questions and discover how these answers vary from one environment to another. And we can still expect that potentially competitive species will sort themselves out among the available environments so that there is a very broad pattern of adaptive tactics in appropriate environments.

In this chapter I shall examine the theoretical answers to tactical questions about reproduction and life-history. For excellent reviews of the supporting data and for abundant references to the exquisite details of behaviour of particular species, see the papers by Stearns (1976, 1977), Southwood (1977), and Stubbs (1977). Other recent reviews of a more technical nature are by Southwood *et al.* (1974), Southwood (1976) and Giesel (1976). Unfortunately, most of the theoretical discussions of tactics of life-history are overloaded with turgid mathematical formalism. Hence, many of the important papers are unintelligible even to the authors of other important papers. Precious

exceptions that are both simple and elegant are the papers by Charnov and Schaffer (1973) and Pianka and Parker (1975), and the short note by May (1977a).

Few of the results in this chapter are new. What is new is the simplicity of their derivation and the compact perspective on the following aspects of adaptive life histories. No formal mathematics are needed to get rigorous results that are free of the restrictive assumptions that traditional approaches entail. In fact the traditional approach has led to an apparent paradox in which different adaptive patterns are predicted depending on whether theoretical models favour growth and survival of populations or bet-hedging in the face of a capricious environment (Stearns 1976). On the one hand, variable environments favour early and copious breeding by lowering the chance that parents will survive to breed in another season; but on the other, variable environments favour spreading a more conservative reproductive output over a longer lifespan because of the high probability of the death of all offspring born in any one season. This paradox disappears when the models explicitly distinguish the opposite effects of juvenile versus parental mortality. The further distinction between adaptation for growth in open environments and persistence in crowded environments is reinforced by positive feedback in selection for both extremes of behaviour. In seasonal environments, adaptations to each season may produce a strategic pattern that is maladaptive to seasonality itself. Dispersal is important not only for denizens of changing habitats, but also for those that live in stable habitats. The study of both the theories and the facts of dispersal in stable and crowded populations has just begun.

The simple derivations have more than heuristic value. Stearns (1977) has recently assembled a lugubrious catalogue of ambiguities and philosophical difficulties that plague the theory of adaptive life-histories. Most of these complications affect the formal development of the theory more strongly than the ideas themselves. Once the ideas are separated from largely unnecessary formal restrictions, they may be explored, in theory and in fact, with fewer philosophical qualms. Stearns has also presented an encyclopaedic review of the places where the available facts fall short of testing theories. These gaps make an excellent shopping list for field work in the future.

14.2 r-selection and K-selection

When a small population is placed in a salubrious environment, it initially grows at an ever increasing pace as more and more individuals

have families who have families; but eventually the population reaches the point where the environment simply lacks the capacity to support more, and it levels at a more or less constant number. Figure 14.1 shows this for a hypothetical population, with a dotted line showing the response of a population with a higher rate of growth, and a dashed line for a population with a higher tolerance of crowding. The population with a higher rate of growth has the numerical advantage at low population sizes or early in population growth. Conversely, higher crowding tolerance is favoured in crowded populations or late in population growth. The extremes that favour growth rate and crowding tolerance are called respectively *r*-selection and *K*-selection. These

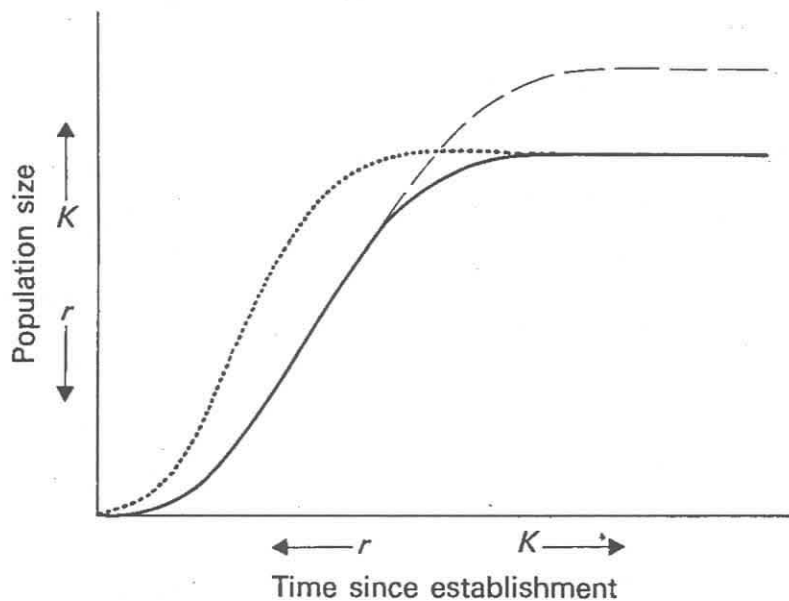


Fig. 14.1. Population growth in a benign but limited environment. The population grows multiplicatively until it reaches the limit of its crowding tolerance. The dotted line shows a population with a higher growth rate (higher *r*); the dashed line, one with higher tolerance of crowding (higher *K*). The axes show population sizes and times at which higher *r* or higher *K* is adaptive.

terms derive from the logistic equation of population growth in a limited environment, in which *r* is traditionally used to represent the rate of growth per capita when the population is sparse, and *K* is the Krowding tolerance, measured as the number or density of individuals at which further population growth is no longer possible. This equation is mathematically tractable and didactically useful even though it is unrealistic in detail. I personally think that the terms '*r*-selection' and '*K*-selection' are barbaric, but they have become commonplace since their introduction by MacArthur and Wilson (1967) to draw together

ideas that had been discussed under many names by many people. I shall keep the jargon as a reminder of how abstract the concepts of *r*-selection and *K*-selection really are.

K-selection favours crowding tolerance via survival, competitive ability, and predator escape, all of which are made easier by large size and parental care, even at the expense of delayed and reduced breeding.

r-selection favours growth rate via fecundity, early breeding, dispersal, and rapid development, all of which are favoured by small size, even at the expense of greater sensitivity to environmental changes.

A benign and constant environment allows population growth to the point at which *K*-selection prevails. However, for *r*-selection to persist, the population must continually be reduced or put back to an early stage of population growth by predation, catastrophes of weather or climate, or the invasion of unoccupied areas. Patchy and insular habitats often provide a continuous supply of local environmental catastrophes and vacant areas for dispersal. Such habitats include true islands and archipelagos, ponds, mud puddles, water in pitcher plants or hollow stumps, open space in forests or in rocky intertidal shores, and edible bundles of food like carcasses, rotting logs, hosts for parasites, and small plants attacked by insects. Thus patchy habitats often combine *r*-selection with selection for dispersal.

14.3 The value and cost of early reproduction

In a classic paper Cole (1954) asserted that an annual animal could become reproductively equivalent to a potentially immortal perennial by adding only one further young to its litter. Cole proved this by a numerical approximation, and other people have contested his result for a variety of reasons, all of which turn out to be wrong.

I shall start by proving Cole's result for an unrealistic case, namely an immortal, parthenogenetic animal who grows to maturity in one year and then has either a single litter or an annual succession of litters, each of equal size. I shall then gradually add the effects of mortality among young, mortality among parents, variation in these mortalities, sexual reproduction, extended time to reach maturity, competition with other members of a growing population, and growth in body size and hence in potential litter size.

To prove Cole's result we need only to observe that if both young and adults are immortal and reproduce asexually one year after the last reproductive period, then there is no reproductive difference

between an adult and any one of its offspring. Hence, adding one more youngster to the litter is a sufficient reproductive gain to offset the loss of all future reproduction by the parent. A visual representation of this proof is shown in Fig. 14.2.

If the young are subject to mortality so that only a fraction Y of them survive their first year, then in order for a parent to assure an additional surviving young at breeding time, the number of young added to the litter must be $1/Y$, since $(1/Y)(Y)=1$.

If parents are also mortal, so that only a fraction P of all parents survive from one annual breeding period to the next, then the probability of annual survival for any given parent is only P . This means that only P young, who survive to breed, need to be added to the litter

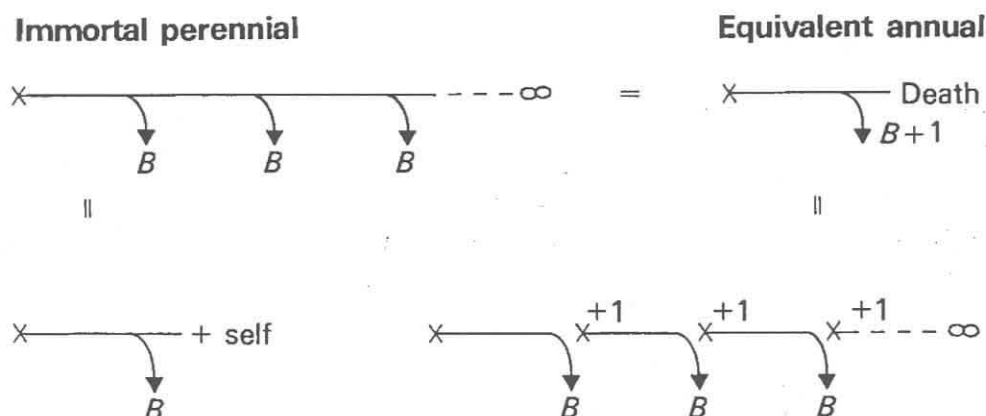


Fig. 14.2. Reproduction of an asexual immortal perennial compared with a more fecund annual. An individual is born at X and then bears B or more offspring at the times indicated by the arrows. That the patterns are reproductively identical is shown by rewriting the perennial's pattern in the format of the annual's and vice versa.

to equal the reproductive potential of the parent. So an annual that bears $B+P/Y$ young and then dies is reproductively equivalent to a perennial that bears B young each year for as long as it lives (Fig. 14.3). This is the conclusion that Charnov and Schaffer (1973) reached, but here it is proved with complete rigour, with fewer restrictive assumptions, and with virtually no mathematics. In particular it is not necessary to assume a stationary age distribution, or even constancy of B , P , and Y beyond the year in question.

We can use the result of Fig. 14.3 to generate adaptive relations between various aspects of life-histories. Massive, early breeding is favoured, even at the expense of death of the parent if a mortal reproductive effort can add more than P/Y young to the litter. This addition is made relatively less expensive if the litter is already large and if the

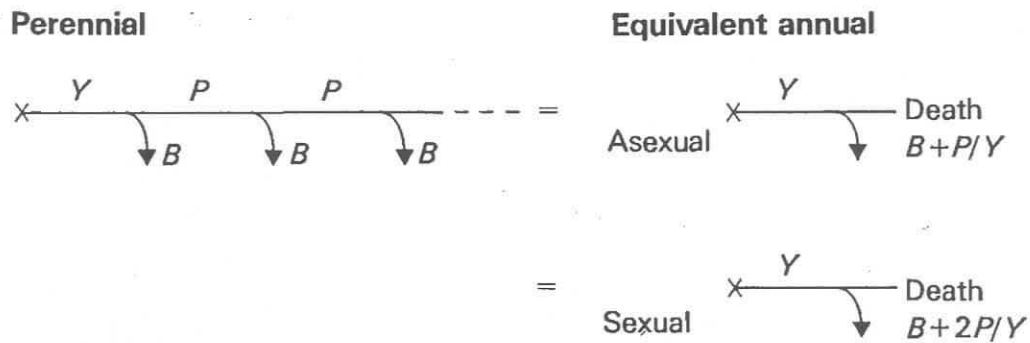


Fig. 14.3. Equivalent reproductive patterns for perennial and annual. This is like Fig. 14.2, but only a fraction Y of the juveniles survive their first season, and only a fraction P of parents survive subsequent seasons. An addition of P/Y young to the litter of an annual ($2P/Y$ for a sexual creature) is reproductively equivalent to potential immortality subject to a survival rate of P per year. The correction for sexual reproduction was derived by Donald Waller and Douglas Green (unpublished manuscript).

offspring are small and require little parental care. Low parental survival (P) and high youthful survival (Y) also lower the expense of the addition since they lower the value of P/Y . Massive reproductive effort will further lower parental survival, so that the selection for early and copious reproduction is self-reinforcing. So the following factors favour early, copious, and self-sacrificial breeding: large litter, small offspring, little parental care, low parental survival, and high survival of juveniles. By converse arguments the factors that favour restrained early breeding and thus survival for iterated breeding are: small litter, large young, parental care, high parental survival, and low survival of young. These lists are the same as those associated respectively with r -selection and K -selection.

For heuristic simplicity I have assumed an asexual population, but now the complications of sex are easy to deal with. For a sexual population even a surviving offspring at breeding time is not genetically equivalent to its parents. In the most extreme case, namely a large and highly outbred population, the young only carry half of the genes of each parent. However, this means that the additional number of young need only be doubled to make a single litter the genetically reproductive equivalent of potential immortality; the number of additional young is $2P/Y$ rather than just P/Y (Fig. 14.3). This is a special case of what Williams (1975) has called the cost of meiosis. My use of the cost of meiosis is independent of the controversy that surrounds the use of the concept to interpret the evolutionary origin of sexuality (Barash 1976b, Maynard Smith & Williams 1976, see also

Chapter 6). For a locally fragmented and inbred population, the number of additional young needed would be something between P/Y and $2P/Y$. All of the qualitative conclusions derived so far for asexual populations remain the same for sexual populations.

To discover the effect of variation in mortality, we must again separate the mortality of adults from that of juveniles. If the survival of parents is variable, the future is further discounted in a way that is closely analogous to lowered average survival of parents. For any survival rate other than 100%, the survival of a given individual is uncertain; if the survival rate is itself subject to unpredictable variation, this uncertainty is compounded. The increased uncertainty of survival to breed again favours early and copious breeding, just as lowered average survival does. Variations in survival of juveniles, especially if they die in batches, favours spreading the risk of reproductive failure among many batches; that is, conservative but iterated breeding. Thus variation in juvenile mortality also has an effect analogous to lowered juvenile mortality, though the line of reasoning is slightly different from the case of parental mortality.

If development is so rapid that maturity is reached in the interval between two reproductive seasons, then offspring of a young parent are already breeding by the next time that their parent breeds. The reproductive value of the parent's first offspring is compounded multiplicatively. However, if there is a very long period of development and adolescence before actual breeding, the reproductive value of the first batch of young is more nearly a simple addition to that of further young, rather than being compounded. Hence earlier and more exhaustive breeding, when it is favoured, is more highly favoured in species with rapid development to maturity than in those with slow development.

Stearns (1976) has provided an elegant test of these ideas by plotting a graph of the average number of seasons in which an individual breeds, against the ratio of average juvenile mortality to average adult mortality, for a variety of birds, mammals, fish, and insects. He found a strong positive correlation over about a sixfold range of both parameters; the species with relatively higher juvenile mortality indeed bred more often. However there was nearly a fourfold scatter of points, and Stearns pleads for more data to decide whether the cause of this scatter is biological or statistical. Southwood (1976) has gathered a more exhaustive and less critical set of relations, showing a correlation between size and generation time, both of which are inversely correlated with rate of population increase.

Although theory suggests that early breeding will often be exhaustive and that delayed breeding will often be repeated, other combinations are fully consistent with the causal machinery of the theory. For example, many birds and mammals have a limited clutch or litter, favouring repeated breeding. If they inhabit ephemeral habitats which favour early breeding, then birds and mammals might be expected to begin breeding as early as possible and to continue breeding for many seasons. The contrary combination of delayed and exhaustive breeding seems confined to beasts with rapid and potentially indeterminate growth in body size and thus in clutch. The most famous example is the sockeye salmon of the Pacific (Foerster 1968) which makes a self-sacrificial breeding effort at an age of three to seven years. Many examples are found among plants, including the spectacular case of a Philippine palm tree in Miami, Florida, which grew quietly for 44 years and then in about 4 months manufactured 300,000 fruits weighing a total of 600 kilograms and displayed on nearly 6 kilometers of stem (Tomlinson & Soderholm 1975). Other examples of unusually late breeding are combined with synchronous breeding of all members of a local population, for example every 13 or 17 years in cicadas (Lloyd & Dybas 1966) or about every 120 years in bamboo (Janzen 1976). In these cases the synchrony, which has been interpreted as a device for overwhelming predators, may be more important than the delay *per se*.

Growth of the population as a whole accentuates the reproductive value of the first batch of young over later batches. For a population that is growing at a per capita rate of r , young born T years in the future should be discounted by e^{-rT} because they will face e^{rT} times as many competitors as those born in the present. This discount for population growth is completely analogous to what economists call 'discounted present value' (Clarke 1976). It was an economic analogy that prompted Fisher (1958) to define the reproductive value of the future offspring of individuals of age x as:

$$\frac{e^{rx}}{l_x} \int_x^{\infty} b_t l_t e^{-rt} dt,$$

where r is the per capita growth rate of the population, b_t is the birth rate to individuals of age t , and l_t is the probability of survival from birth to age t . This recipe for reproductive value is used in many technical analyses of life-histories; so I shall explain it even though I shall not use it. Fisher's original definition was telegraphic, and most

recent explications are opaque; so it is useful to rewrite Fisher's formula in a readily interpretable form:

$$\int_x^{\infty} b_t(l_t/l_x) e^{-r[t-x]} dt.$$

In this form reproductive value is clearly the sum into the future from age x of (reproductive output at a future age) (probability of reaching that future age from age x) (discount on future reproduction for growth in number of competitors in the population between age x and that future age). Pianka and Parker (1975) partition this reproductive value into current and future components and graphically analyse the tactical partitioning of reproductive effort into current reproduction versus survival for later reproduction. Their results are more detailed than those developed here, but not qualitatively different.

The effect of a declining population is slightly more complex. If the decline is due primarily to juvenile mortality, delayed breeding is favoured since future offspring will face fewer competitors than present offspring. If the decline of the population involves heavy mortality among adults, then the competitive value of delayed reproduction may be offset by the low probability of the potential parent's surviving a delay. If the population is steady, then age of reproduction *per se* is irrelevant, though any parent whose offspring carry some other competitive advantage like higher tolerance of crowding can augment this competitive advantage by breeding early.

The effect of parental growth in size and experience is easy to state in a qualitative fashion, but the recipes for calculating it are horrendous. The effect depends on whether growth in potential size or success of the litter exceeds the compound interest growth of fewer or smaller young invested in the population earlier. Simply put, delayed breeding and growth are favoured if the potential growth of a population of offspring within the body of the parent exceeds the potential growth of the population of offspring in the environment outside of the parent.

Schaffer and Elson (1975) have analysed the interaction of growth and mortality in determining adaptive timing of spawning by Atlantic salmon in different North American river systems from Maine to Ungava. These fish are born and spend their youth in rivers and streams, live through adolescence and adulthood in the sea, but return to their home rivers to spawn. In contrast with the Pacific salmon, their spawning is not exhaustive, and they may return to spawn again after a further period at sea. The mean age of first spawning is greater in the

harsher rivers that forbode greater mortality for smaller fish. Commercial fishing increases the death rate of larger and hence older fish and thus favours earlier spawning. Conversely, rapid growth at sea favours delayed spawning. All of these observations are consistent with the theoretical expectations.

Perhaps the most important result of this section is that juvenile mortality and parental mortality have opposite effects on the prediction of adaptive tactics. Juvenile mortality biases toward K -selection, but adult mortality biases toward r -selection. There is really nothing subtle about this difference. Since the only reproductively effective offspring are those who reach maturity and breed, pre-reproductive mortality can be viewed as subtracting from the ultimately effective natality of the parent (Charnov & Schaffer 1973). In a sense, juvenile survival enters the analysis as though it were simply birth rather than survival itself. The effect of variation in mortality also differs for juvenile and parental mortality; and the effect of increased variation is analogous to lowering the respective average survivals. We obtain fully concordant results from an analysis of either average mortality or unpredictable variations in mortality; the paradox discussed by Stearns (1976) disappears. The dichotomy is rather whether environmental mortality falls more heavily on juveniles or adults.

Any increase in reproductive effort is likely to weaken a parent and to increase its subsequent risk of mortality, which in turn favours a further increase in current reproduction. Such self-reinforcing selection will be discussed when r and K selection are revisited. Because reproduction and survival are interdependent it is not always possible to design an optimal life history by exploring the effect of changes in reproductive behaviour. In addition to being mathematically difficult (Mirmirani & Oster 1978) or messy (Schaffer & Rosenzweig 1977), a general analysis may yield several sets of tactics that are better than anything close to them, or it may produce optimal tactics that cannot be attained. Such technical difficulties and biological ambiguities are details beyond resolution in the broad picture of this chapter, but they will surely provide interesting theoretical insights in the future.

14.4 Fluctuating reproduction in a fluctuating environment

If the quality of the environment fluctuates more or less regularly on a cycle that is not greatly shorter or longer than an animal's life-span, the appropriate strategy is reproduction during periods of boom but

survival during periods of bust. Moreover, MacArthur (1968) used an ingenious graphical model to show that the rate of reproduction averaged over the whole environmental cycle is higher if there are extreme shifts between profligate breeding and dogged survival, than it is for a moderate response. MacArthur's analysis is repeated in Fig. 14.4.

There is an inevitable lag in the response of an animal to changes in its environment, particularly if the response requires a shift from physiological mobilization of resources for reproduction to storage for survival, or vice versa. The lag and the shift itself virtually guarantee that a population whose members are adapted to environmental fluctuations will continue to undergo drastic fluctuations in population size even during periods of relatively steady environmental conditions. These fluctuations in population size can be viewed as fluctuations in degree of crowding, to which the appropriate adaptation is yet more extreme shifts in reproductive behaviour, reinforcing a vicious cycle.

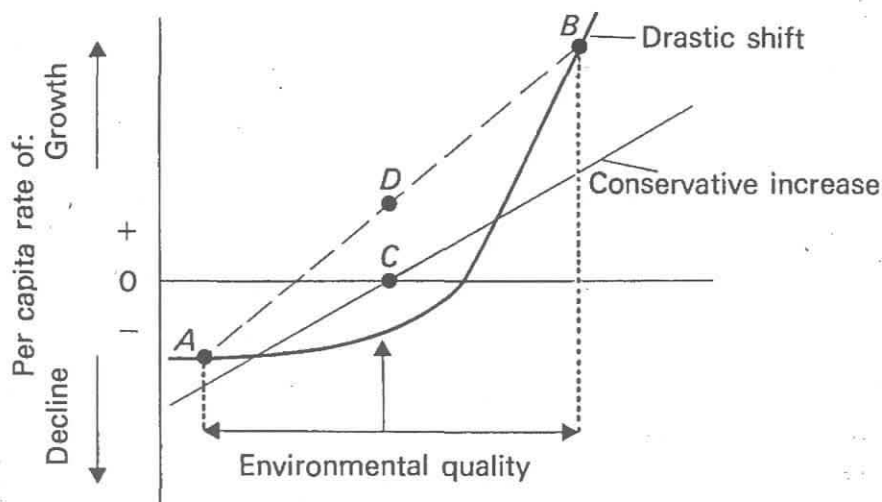


Fig. 14.4. Reproduction in a fluctuating environment. Two kinds of response to environmental quality are compared: a conservative increase in growth rate with increasing environmental quality, and a drastic shift from profligate breeding in good times to dogged survival in poor, at the expense of lowered growth in average conditions. In an average and constant environment (vertical arrow), the conservative response yields the higher rate of growth. However, if the environment shifts back and forth between sufficiently different extremes (horizontal arrows and dotted lines), while preserving the same average, then the average growth rate is a linear average of the extreme growth rates (e.g. of A and B), and it can be graphically calculated as the point at which a straight line between the extreme growth rates crosses the average environmental quality. The average growth rate for the drastic response (D) is higher than that of the conservative response (C) in a sufficiently variable environment (MacArthur 1968).

A peculiar pattern is common to empirical studies of cyclic populations of caterpillars (Wellington 1960), voles (Krebs *et al.* 1973), and locusts (summarized by Krebs 1972). As the population fluctuates in any given location, its composition alternates between primarily dispersive and primarily sedentary individuals. This shift in composition is itself enough to generate and to maintain the cycles of local population size. The data have yet to be considered from the opposite point of view; namely, to what extent are the cycles instrumental in selecting for the reproductive characteristics that generate them? More detailed theoretical discussions in the context of these examples can be found in Schaffer and Tamarin (1973) and May (1977b).

The famous examples of dramatic cycles in population size are small, ravenous herbivores. However, the arguments apply with equal force to nearly all of the species that inhabit a strongly seasonal environment and that grow to reproductive maturity in a single season. Furthermore, even the most mathematically simple models of population growth that include a lag in response show violent cyclic and even chaotic behaviour in a constant environment, as long as the potential rate of growth is sufficiently high (May 1976 pp. 11–17). Hence reproductive adaptations to a fluctuating environment may be important even in species that are not well known for regular cycles in population size.

14.5 Dispersal

In an environment that changes in quality from time to time, there are two ways to avoid the effects of hard times. One is to endure them locally; the other, to migrate to a better place. Migration or dispersal of young is most favourable when the pattern of environmental fluctuation varies from place to place, since there will often be another place where conditions are better (Fig. 14.5). However, if the environmental changes are highly correlated from place to place, then hard times in one place mean hard times in another, and endurance, even to the point of dormancy or diapause, is favoured over dispersal. Thus one expects dispersal as an adaptation to local vagaries of weather, competition, predation, and patchy changes in the plant community; but dormancy in response to seasonal and other broad climatological changes. A more detailed discussion is given by Gadgil (1971).

It is no surprise that dispersal should be advantageous when the local environment is deteriorating, but Hamilton and May (1977) have recently argued that it is adaptive for parents to enforce dispersal of

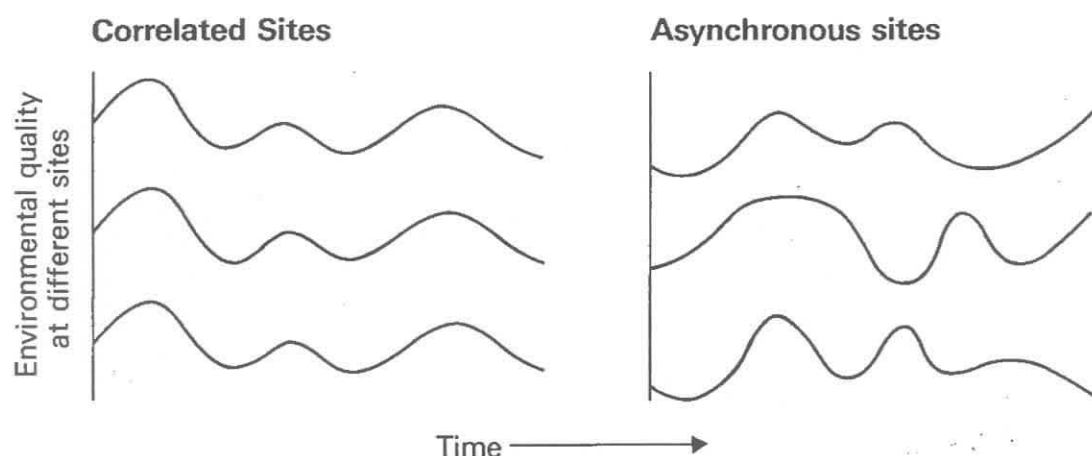


Fig. 14.5. Fluctuations in environmental quality at different sites. Where conditions are correlated from site to site, dispersers cannot improve their lot by moving; and local endurance, dormancy, or diapause is favoured. Where different sites fluctuate asynchronously, dispersal during bad times offers some chance of encountering better conditions elsewhere.

some of their young even in an environment that is crowded, but otherwise steadily healthy. Hamilton and May envision an environment that is crowded with sessile adults whose offspring compete within their own generation for the spaces vacated by the deaths of adults. Offspring who do not disperse must compete for their parent's site with both siblings and the dispersive offspring of other families. Therefore any parent whose entire family remains to compete for its space stands a finite chance of leaving no issue if any other members of the population have dispersive offspring; and it has no chance whatsoever to have more than one surviving offspring in the next generation. Dispersal of at least some offspring lowers the probability of total reproductive failure, and it gives a parent a more even chance in competition, with other parents of dispersive young, for placement of young in new vacancies. Hamilton and May discuss the complications that ensue when the strategy of dispersal that is optimal for parents is not optimal for their offspring, and they agonize over the restrictive assumptions of their model, but their main conclusion seems robust. It is advantageous for parents to enforce some dispersal by their offspring even when the local environment is not deteriorating and even when the process of dispersal itself incurs considerable mortality. Van Valen (1971) has presented a similar model showing the adaptive value of dispersal from local populations rather than families, over evolutionary spans of time rather than ecological.

14.6 *r* and *K* selection revisited

The major results of this chapter can be summarized in two diagrams that show the causal relations among environmental fluctuations, dynamics of populations, and aspects of natural history. Such diagrams are given for the extremes of *r*-selection and *K*-selection in Figs. 14.6

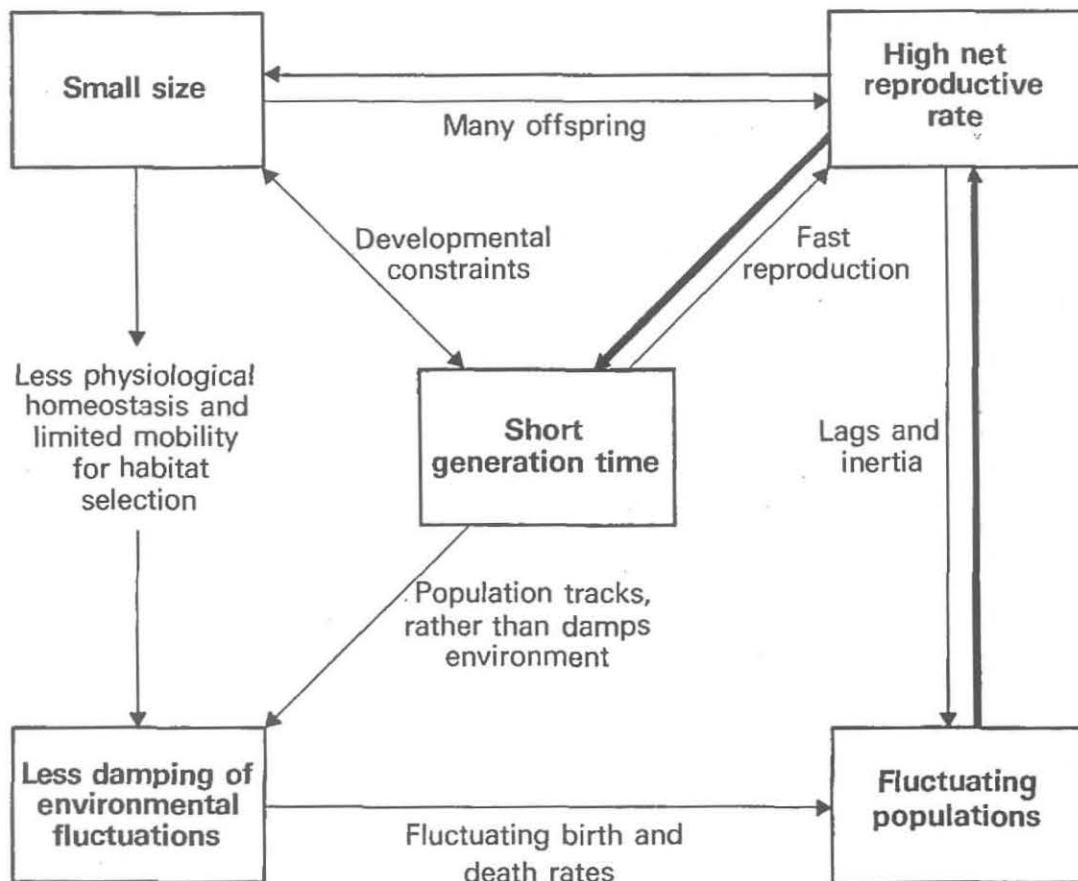


Fig. 14.6. Positive feedback loops reinforce *r*-selection. This is a summary of the relations among aspects of life-history, with arrows pointing from causes to effects that are discussed in the text. The heavy arrows represent actual selection. The idea of making this diagram is pilfered from Southwood (1977).

and 14.7. The diagrams also indicate the primary pathways by which selection favours rate of growth in one case and crowding tolerance in the other. Two additional relations in the diagram have not been discussed yet, but they are straightforward. Size is correlated with life-span or generation time, in part because smaller beasts live a more frenetic life and wear themselves out faster, and in part because it takes

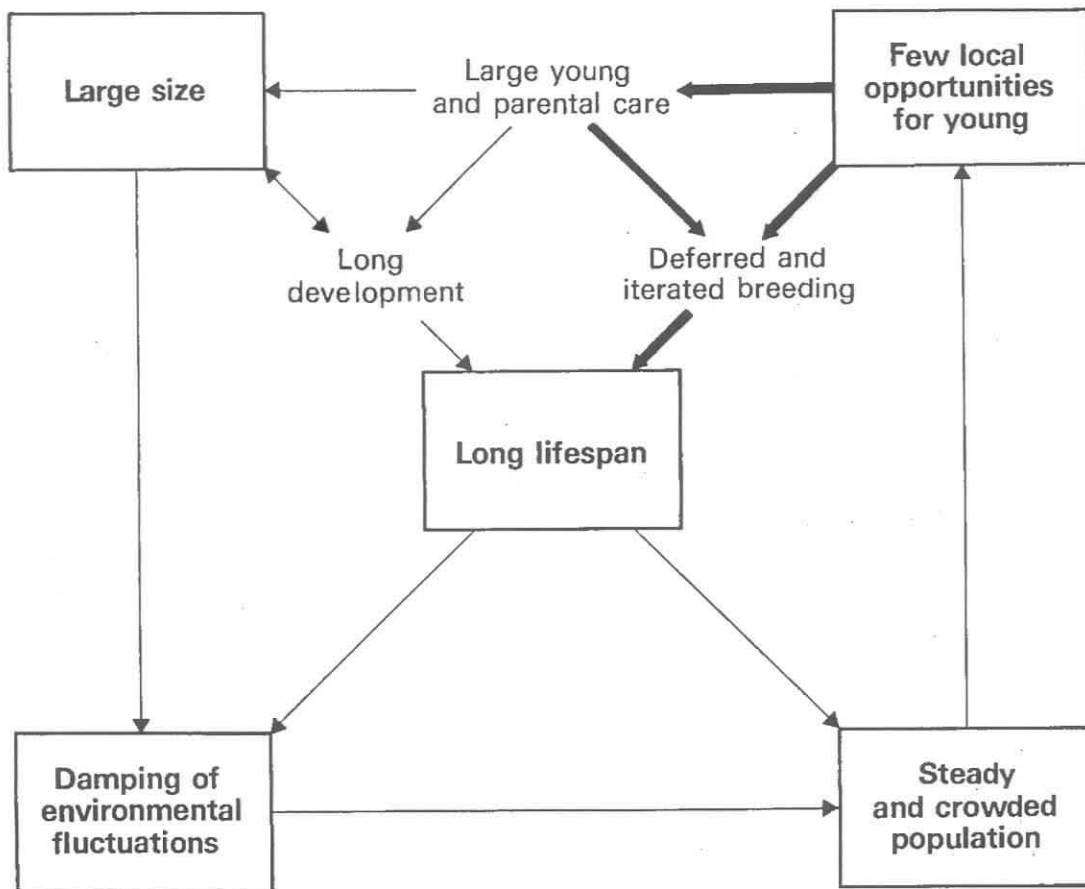


Fig. 14.7. Positive feedback loops reinforce *K*-selection. Some of the effects in this diagram are just the converse of those in Fig. 14.6, but the two diagrams are different in important respects that are discussed in the text.

longer to grow bigger. Small adult size implies greater sensitivity to environmental fluctuations, because small beasts cannot move easily to a new habitat when faced with local adversities, and though they may compensate by finding tiny hiding places where many physical fluctuations are damped, they are more sensitive to these physical fluctuations because of their small specific heat capacity and large ratio of surface to volume.

The first lesson of Figs. 14.6 and 14.7 is that *r*-selection and *K*-selection are both self-reinforcing. For example, selection in a fluctuating population favours a high reproductive rate, which is made easier by small size and a short generation time, which in turn reduces the ability of the population to damp environmental fluctuations, which increases the fluctuations in the population, further favouring a high reproductive rate, and so on. This positive feedback for both extremes of *r*-selection and *K*-selection suggests that animals in nature may show

extreme characteristics more often than an intermediate set of characters. Perhaps this is a biological reason for the smouldering controversy over the mechanisms of population regulation in animals (Stubbs 1977, McLaren 1971).

Comparing Figs. 14.6 and 14.7, it is tempting to suggest that small animals are subject mainly to r -selection, and large animals to K -selection. There is enough truth in this suggestion for it to be a major tenet of modern ecology, but there is enough triviality in it to warrant scrutiny. Southwood and friends (1974) have noted the importance of relating the temporal scale of changes in the environment to the scale of the generation time of the animal. If environmental changes occur within a few generations, r -selection prevails. If the environment changes slowly over many generations, K -selection prevails. In complete ignorance of environmental effects, one can trivially state that most large animals will delay reproduction until they grow to be large. They may also be insensitive to environmental fluctuations that would destroy smaller animals, but they may be just as sensitive as the small beasts to longer term fluctuations that are commensurate with their lifespans. Stubbs (1977) has elegantly analysed data from a variety of animals, and found that mammals and birds are indeed dominated by K -selection, as befits large animals. However, she found that insects have some species whose life histories are dominated by r -selection, and some species dominated by K -selection.

The second lesson is that the diagrams of Figs. 14.6 and 14.7 are not simply the converse of one another. This hints that r -selection and K -selection are not simply opposite ends of a one-dimensional spectrum. In particular, the introduction of dispersal into population models has dramatically different consequences for r and K selection. Dispersal further reinforces r -selection because an abundance of small offspring is favourable for dispersal, and the mortality incurred by dispersal of young further increases the value of early and copious breeding. However, the introduction of dispersal into the diagram for K -selection may change its topology entirely. If dispersal provides youngsters with opportunities for colonization at some distance from their place of birth, then the fact that there are few local opportunities for them is less important, and the positive feedback loop that reinforces K -selection is broken. A whole new series of tactical questions is opened. Should many small young be broadcast at random? Should fewer young be sent out to seek their fortunes with a heavy grubstake from their parents? Should offspring remain at home and engage in territorial feuds with neighbouring clans? Should offspring look for vacancies or

fight to create them? These questions need tactical answers before we can guess what mixture of tactical responses to K -selection and r -selection is the appropriate strategy for individuals in a crowded and steady population.

Figure 14.8 shows the relation between r and K selection at yet a further level of abstraction. In a given locality, population growth will turn r -selection into K -selection unless predation or regular catastrophes keep populations well below the capacity of the environment.

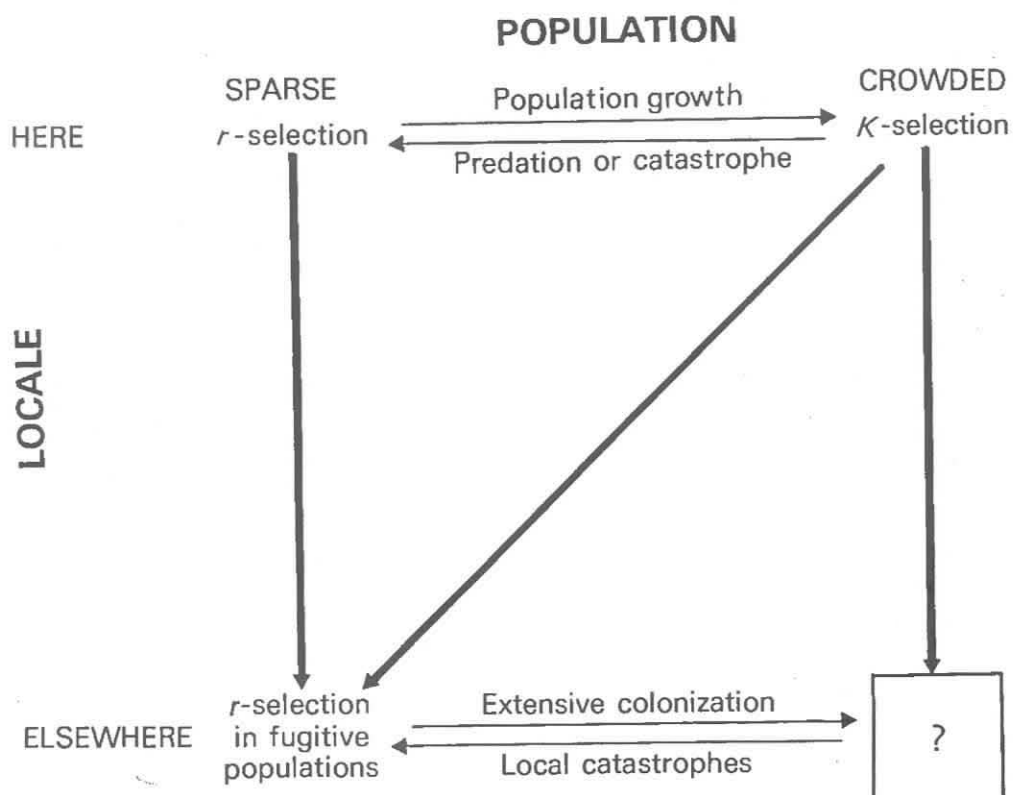


Fig. 14.8. Relations among r -selection, k -selection, population density, and dispersal. The heavy arrows represent dispersal. The big question mark indicates a critical gap in current theories.

Then the tactics of reproduction *per se* are less interesting than the adaptive response to predators or the ways of surviving or recovering from catastrophe (Wilbur *et al.* 1974). If a parent ensures the success of its descendants by sending them off to colonize newly vacant places, then r -selection continues indefinitely, but again the tactical machinery of dispersal may be of as much interest as reproduction itself. This may be why Southwood's (1977) list of synonyms of r -selection includes terms like fugitive species, opportunists, pioneers, and super tramps.

Dispersers from a crowded population may land in an uncrowded environment, in which case the adaptive life history may include

elements favoured by r -selection and K -selection. However, if the dispersers land in a crowded population in another locality, adaptive tactics have yet to be explored by behavioural ecologists. It is not even clear whether dispersal may be favoured in globally crowded populations of motile species. Although the specific model of Hamilton and May (1977) does not apply, similar ideas could be developed in this context. In particular, in a crowded population of sedentary, long-lived adults, vacant territories due to recent deaths will be rare and scattered. Dispersal, especially in the form of itinerant adolescence, could expose youngsters to a large number of potential vacancies, even at the expense of encountering young competitors who are also looking for those same openings.

Woolfenden and Fitzpatrick (1978b) present a novel and exemplary analysis of dispersal in Florida scrub jays, mapping the dispersal of young of known parentage in a patchy and crowded environment. Male and female offspring both remain on their parents' territory, help to defend it, and assist in the feeding of the next batch of siblings. Females tend to spend a year or two helping while exploring widely in search of suitable mates and territories. Males stay at home for as much as three to five years, often extending their family's territory at the expense of adjacent families. A male helper then tends to 'bud off' his own territory from his father's, or to move quickly into any nearby vacancy. Thus in the face of the same crowded environment, males and females find breeding territories by very different patterns of dispersal (see also 3.5.2 and 9.2).

The tactically adaptive form of dispersal depends on the context. If adults can actively select habitats, then adults should disperse and leave well-provisioned offspring in appropriate places. If adults cannot move about or select habitats, they must broadcast young over both appropriate and inappropriate habitats. The first case is consistent with K -selection; the second entails very low survival of young, and therefore accords more with r -selection. The two cases have very different consequences for habitat selection, population dispersion, kinship structure, outbreeding, and even the adaptive significance of sex.

Wilbur (1977) has discussed these alternatives in the context of an engaging juxtaposition of data from salamanders and milkweeds. His four species of salamanders breed in ponds of varying size and persistence. Females of each species disperse their eggs in different ways, from one big bunch through several bunches, to singly or in pairs. The differences in dispersion are apparently adapted to patterns of larval survival in ponds that differ in persistence and predatory regime. The

parents of milkweed seedlings cannot move about, but they can adjust the dispersal of their offspring through the number and timing of seed pods, and the size and number of seeds in each pod. Wilbur's six species of milkweeds show the same range of adjustments in dispersion of offspring as do his salamanders. However, he did not document any differences in the milkweeds' habitats to which these reproductive attributes might be adaptive.

There is a whole series of tactical questions about dispersal that have barely been asked, let alone been answered. Should adults disperse? Should young disperse? Should the tactics of parents and offspring agree? How should the tactics of dispersal vary with the level of crowding within a local population? I began with questions; I have ended with questions. It is a measure of progress that the two lists of questions are different.